



Avian Behavior, Ecology, and Evolution

Do larids exhibit sex-biased natal dispersal? A case study of a southwest Florida population of Black Skimmers (*Rynchops niger*)

¿Presentan los laridos una dispersión natal sesgada por sexo? Un estudio de caso de una población del suroeste de Florida de Rayadores negros (*Rynchops niger*)

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ABSTRACT. Understanding dispersal patterns in a species provides important evolutionary and ecological knowledge. Dispersal decreases inbreeding, which can greatly influence a species' genetic diversity and conservation status. We examined natal dispersal sex differences in a southwest Florida population of Black Skimmers (*Rynchops niger*) by collecting band resighting data from 86 (57 males, 29 females) skimmers during the 2017–2022 breeding seasons. We examined sex biases in the proportion of natal dispersers and the distances traveled from their natal colonies. The majority of skimmers dispersed (72% of females, 61% of males), however, no statistically significant difference was found between the proportion or distance traveled between the sexes. As beach habitat becomes fragmented by development and sea level rise, the ability of both sexes to disperse may benefit both Black Skimmer genetics and demographics in a changing world.

RESUMEN. Comprender los patrones de dispersión de una especie proporciona importantes conocimientos evolutivos y ecológicos. La dispersión disminuye la endogamia, lo que puede influir enormemente en la diversidad genética y el estado de conservación de una especie. Examinamos las diferencias en la dispersión natal de cada sexo en una población del suroeste de Florida de Rayadores negros (*Rynchops niger*) mediante la recopilación de datos de reavistamiento de bandas de 86 individuos (57 machos, 29 hembras) durante las temporadas de cría 2017–2022. Examinamos los sesgos de sexo en la proporción de dispersores natales y las distancias recorridas desde sus colonias natales. La mayoría de los rayadores se dispersaron (72% de las hembras, 61% de los machos), sin embargo, no se encontraron diferencias estadísticamente significativas en la proporción o la distancia recorrida entre los sexos. A medida que el hábitat de la playa se fragmenta por el desarrollo y el aumento del nivel del mar, la capacidad de dispersión de ambos sexos puede beneficiar tanto a la genética como a la demografía del Rayador negro en un mundo cambiante.

Key Words: *Black Skimmer*; *natal dispersal*; *Rynchops niger*; *sex bias*

INTRODUCTION

Studying philopatry and dispersal is vital for understanding the evolutionary biology, ecology, and conservation of birds. Natal philopatry describes the return of an individual to its natal site to breed (Coulson 2016, Antaky et al. 2021), although dispersal refers to either an individual's movement between birth and their first reproductive event (natal dispersal) or the subsequent movement of an individual between breeding sites (breeding dispersal; Greenwood and Harvey 1982). Motivations for dispersal include the avoidance of inbreeding and intraspecific competition (Danchin and Cam 2002, Coulson 2016, Acker et al. 2018) as well as the movement to a better-quality habitat with more resources (Spear et al. 2002, Antaky et al. 2021). However, moving to a new territory means a lack of familiarity with available resources and potential predators, which exposes individuals to threats such as failed reproduction or mortality (Renken and Smith 1995, Coulson 2016, Antaky et al. 2021).

Avian dispersal tendency is typically biased toward females (Greenwood and Harvey 1982, Clarke et al. 1997, Mabry et al. 2013), both in proportion and distance traveled (Clarke et al. 1997, Végvári et al. 2018). One of the most common hypotheses explaining primarily female biased dispersal is that males of many species are the more territorial sex and therefore more concerned

with the defense and care of their territory so that they may attract mates (Greenwood 1980, Greenwood and Harvey 1982). However, the exact origins of sex-biased dispersal are still debated and there does not appear to be one hypothesis that sufficiently captures the explanation for the sex differences (Greenwood 1980, Clarke et al. 1997, Mabry et al. 2013). Also, the mechanisms that drive sex bias in natal dispersal might not necessarily match those that impact breeding dispersal, so natal and breeding dispersal should be analyzed separately (Végvári et al. 2018).

Historically, it was assumed that most seabirds exhibit a high level of philopatry, however, this assumption may be biased because it is easier to identify individuals that have stayed compared to those that moved (Coulson 2016). Larids (gulls, terns, and skimmers) are primarily monogamous, colonial, or semi-colonial seabirds that nest in coastal areas (Winkler et al. 2020). Only 16 of 97 larid species from Winkler et al. (2020) have publications involving natal dispersal, and only 6 have data regarding sex-biased natal dispersal. Female-biased natal dispersal has been found in the Black-legged Kittiwake, *Rissa tridactyla* (Coulson and Nève de Mévergnies 1992), the Western Gull, *Larus occidentalis* (Spear et al. 2002), the Herring Gull, *Larus argentatus* (Chabrzyk and Coulson 1976), and the Common Tern, *Sterna hirundo* (Becker et al. 2008).

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Female-biased natal dispersal in larids may exist because males are more involved in the acquisition and maintenance of the nesting territory, although females explore other colonies in search of the best mate (Spear et al. 2002, Becker et al. 2008). Additionally, higher productivity has been found in female Western Gulls that disperse, so reproductive success could be another explanation for female-biased natal dispersal (Spear et al. 2002). Our objective is to examine sex-biased natal dispersal in Black Skimmers (*Rynchops niger*) within southwest Florida to identify if natal dispersal tendency and distance differed between the sexes.

Black Skimmers are colonial-nesting larids that primarily breed on open beaches along the Atlantic and Gulf coasts of the United States (Gochfeld et al. 2020). This species is sexually dimorphic with males weighing more and having longer tarsus, culmen, and wing chord lengths than females (Quinn 1990, Forsys et al. 2022a). Skimmers are monogamous and both sexes share parental responsibilities when caring for chicks. Pairs establish small territories within the colony at the beginning of the breeding season. Although both sexes defend the territories from conspecifics, males are responsible for significantly more of the aggressive encounters than females (Burger 1981). Because of a significant decline in the number of skimmers along with current threats from habitat loss, and disturbance and predation, the species is listed as threatened within the state of Florida (FWC 2022). Getting information on the frequency and sex bias of dispersal in the Black Skimmer is vital data for models that will help manage this species.

METHODS

Study area

We studied skimmers that were hatched and banded on beaches in Pinellas County, Florida (27°54'00.0" N, 82°44'00.0" W) a peninsula in West Central Florida, bordered by the Gulf of Mexico and Tampa Bay (Fig. 1). Pinellas is a highly urbanized county, and Black Skimmer colonies are easily accessible because they are often on busy public beaches. Banded skimmers were resighted throughout Florida and surrounding states.

Most of the skimmer colonies occurred on barrier islands connected to the mainland via bridges. Three relatively large and accessible colonies occurred on these developed barrier islands: Clearwater Point, Indian Shores, and St. Pete Beach (Fig. 1). The colonies have shifted slightly among breeding seasons, but none moved more than 1.5 km. Clearwater Point is a private beach behind a condominium complex that experienced very few human-related disturbances (Forsys et al. 2022b). Indian Shores is located on a more crowded beach next to condominiums and a volleyball court, which are frequently used by tourists. St. Pete Beach is a heavily trafficked public beach that borders hotels and condominiums. All three colonies were protected by bird stewards who educate the public and decrease human disturbance (Forsys et al. 2022b). Numbers of pairs and nests fluctuated among colonies and years, but maximum nest count ranged from 85-255 (Table 1). Productivity was variable but was similar to other published studies of North American colonies (Gochfeld et al. 2020).

Fig. 1. Study area map displaying the three Black Skimmer (*Rynchops niger*) natal colonies of the individuals used in the study and the southwest Florida skimmer colonies to which they dispersed. All three natal colonies were also considered dispersal colonies, as some of the skimmers moved between those natal colonies.



Data collection and analysis

During 2015 to 2019, a total of 225 3-4-week-old Black Skimmer chicks were caught using hand nets at the 3 Pinellas County natal colonies (Clearwater Point, Indian Shores, and St. Pete Beach) and banded with 12- or 20-mm field readable bands. Banded birds were resighted from 2015-2022 by members of the Florida shorebird alliance (FSA), a network of volunteers, biologists, and beach managers that is committed to advancing shorebird and seabird conservation in Florida (FWC 2022). Trained surveyors followed Florida's breeding bird protocol at colonies at least once each week and recorded the number of nests, chicks, adults, and any banded birds and entered this data into the Florida shorebird database (FSD 2022). For example, in 2022, the 42 skimmer colonies in Florida were officially monitored 586 times (FWC 2022). Additional band resightings came from FSA monitoring outside the official surveys, members of the public who found our web and Facebook pages, as well as partners who monitor skimmers through the Gulf and Atlantic Coasts. Some colonies were surveyed for bands more than others, but all colonies were monitored several times each month.

The natal colony of each bird was recorded when it was banded as a flightless chick. We recorded the locations where each banded skimmer was seen breeding for the first time to compare to their natal colonies. Banded skimmers were only included in our data if they were observed to be mating or incubating. Black Skimmers do not reach sexual maturity until their second or third year

Table 1. Productivity data for the three natal Black Skimmer (*Rynchops niger*) colonies in Pinellas County, Florida from 2015-2019, including the number of banded birds that were philopatric and the number that dispersed to breed at a new colony.

Year	Natal Colony	Max Nests (n)	Max Fledglings (n)	Productivity (fledgling/nest)	# Philopatric	# Dispersed
2015	Clearwater Point	150	125	0.83	0	0
	Indian Shores	250	55	0.22	2	3
	St. Pete Beach	148	169	1.14	6	8
2016	Clearwater Point	254	146	0.57	0	0
	Indian Shores	90	33	0.37	0	2
	St. Pete Beach	92	103	1.12	3	7
2017	Clearwater Point	180	177	0.98	3	5
	Indian Shores	85	169	1.99	1	4
	St. Pete Beach	135	236	1.75	5	6
2018	Clearwater Point	65	41	0.63	0	0
	Indian Shores	70	34	0.49	3	3
	St. Pete Beach	230	149	0.65	4	2
2019	Clearwater Point	128	91	0.71	1	3
	Indian Shores	152	85	0.56	1	6
	St. Pete Beach	250	227	0.91	1	7

(Gochfeld et al. 2020), so the earliest a skimmer could be observed and recorded to be breeding would be two years after hatching. Hence, even though the skimmers were banded during 2015-2019, our study represents data collected during the 2017-2022 breeding seasons (May 15-September 15).

In total, of the 225 flightless chicks we banded, we determined the first breeding location for only 86. Twenty individuals died before leaving the colony, primarily during a salmonellosis outbreak associated with the release of raw sewage in 2016 (Shender et al. 2022). Many banded birds were not seen after fledging, but the majority of the birds seen after their first year were seen frequently in subsequent years. Throughout their range, skimmer survival from the time of fledging to year one is believed to be low, although skimmer adult survival is generally very high (Gochfeld et al. 2020).

Profile photographs of the 86 Black Skimmers used in our analyses were taken once they were adults, and sex was determined using a verified method described by Forsys et al. (2022a). Of the 86 skimmers, we identified 29 females and 57 males. The dispersal distances between the skimmers' respective natal and breeding colonies were measured by drawing a straight line between the

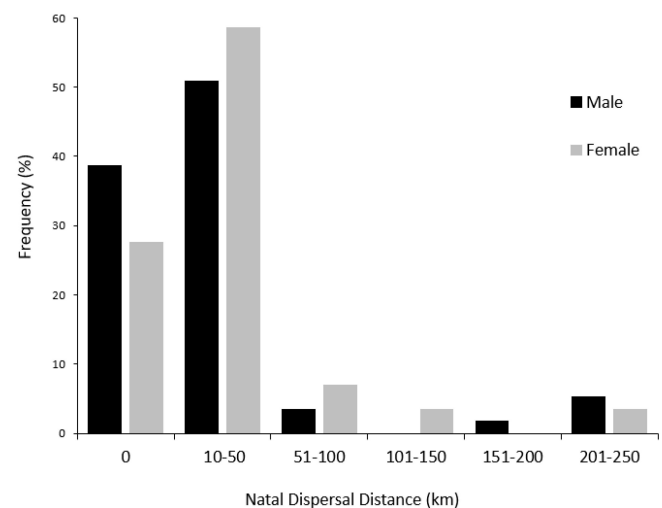
two colonies using ArcGIS Pro v.2.8.1 (ESRI 2021). Birds were considered philopatric if they nested at their natal colony (dispersal distance = 0 km). The three natal colonies (St. Pete Beach, Indian Shores, and Clearwater Point) were also considered dispersal colonies because some skimmers moved between these colonies. Statistical tests were done using R v.4.2.1 (R Core Team 2022). To determine if the proportion of female natal dispersers differed significantly from males, we conducted a chi-square test of independence. To test for a difference between the dispersal distances of the dispersers for each sex, we used a Wilcoxon rank sum test because our data were not normally distributed ($p < 0.05$).

RESULTS

About 72% of females dispersed compared to 61% of males (Fig. 2), and this difference was not significant ($\chi^2 = 0.60$, $P = 0.44$). Natal dispersal distances ranged from 12.9 - 242.6 km (Fig. 2). On average, female natal dispersers traveled 43.8 km (median = 27.2 km, range = 15.3 - 217.9 km), while males traveled 51.4 km (median = 27.2 km, range = 12.9 - 242.6 km). Natal dispersal distance did not differ significantly between the dispersers of each sex, 35 males, and 21 females ($W = 354$, $P = 0.59$).

Of the 86 Black Skimmers that dispersed, 81% of females and 83% of males traveled ≤ 50 km from their natal colony (Fig. 2). The proportion of skimmers that dispersed was similar among each of the three natal colonies (61% from St. Pete Beach, 72% from Indian Shores, and 67% from Clearwater Point). See Tables 1-2.

Fig. 2. Percentages of male ($n = 57$) and female ($n = 29$) Black Skimmers (*Rynchops niger*) with their respective distances they traveled from their natal colony to their dispersal colony (km).



DISCUSSION

We found that over half of all skimmers exhibited natal dispersal, and the proportion that dispersed was similar for males and females. In addition, we did not find a statistically significant difference between the natal dispersal distances for each sex. The majority of both males and females that dispersed moved to colonies within 50 km of their natal colony. A similar proportion

Table 2. Count of banded Black Skimmers (*Rynchops niger*) that either nested at their natal colony where they were banded, or moved from one of the three natal colonies (St. Pete Beach, Indian Shores, and Clearwater Point) to one of the dispersal colonies where they bred for the first time.

Dispersal Colony	Natal Colony		
	St. Pete Beach	Indian Shores	Clearwater Point
St. Pete Beach	19	11	0
Indian Shores	6	7	5
Clearwater Point	4	1	4
3D	1	1	0
3 Rooker	0	1	1
Carlos Point	1	1	0
Caxambas Pass	0	1	0
Egmont Key	2	0	0
Lido Key	13	2	1
Longboat Key	0	0	1
Marco Island	1	0	0
Patrick Airforce Base (rooftop)	1	0	0
Stump Pass	1	0	0
Total	49	25	12

(3% of females and 5% of males) dispersed > 200 km. This skew in dispersal distance where only a few individuals travel far from their natal colony has also been recorded in other avian species (Sutherland et al. 2000, Spear et al. 2002, Luna et al. 2020). Overall, our natal dispersal proportion and distance findings are compatible with those from Delgado et al. (2020), who found no sex bias for Yellow-legged Gulls in either natal dispersal proportion or distance traveled. Our findings support Coulson's (2016) claims that philopatry and dispersal vary widely between bird species and that philopatric tendencies in seabirds may not be as high as what was previously thought due to limitations in recapturing birds that travel great distances (Koenig et al. 1996).

Our research has implications for the conservation and management of Black Skimmers. Seabirds, such as Black Skimmers, exist as a metapopulation of individual colonies that are connected in terms of demographic and genetics through dispersal (Oro 2003). Fortunately, finding that over half of the male (61%) and female (72%) Black Skimmers in this study dispersed is advantageous for their genetic diversity and the prevention of inbreeding. Declining species that experience habitat fragmentation and loss can be more susceptible to inbreeding and low genetic diversity, but a high level of dispersal can counteract this (Dayton and Szczys 2021, Rönkä et al. 2021). In addition, dispersing individuals can genetically and demographically “rescue” declining colonies by adding individuals and because both males and females disperse, colonies are less likely to have sex ratio imbalances that would decrease productivity for a monogamous species (Yannic et al. 2016).

The finding that most male and female natal dispersers in our study dispersed no more than 50 km from their natal colonies and most of them dispersed to the south is potentially important for future population viability models. Although southwest Florida supports the largest number of Black Skimmers in the state (Fig.

1), there are colonies in northern Florida, and 14 of the 86 Black Skimmers in our study have spent time outside of the breeding season near some of these colonies, but there is no record of them nesting. This low level of dispersal to the north might be important if skimmer populations continue to decline. This study shows the locations of where Black Skimmers in southwest Florida are dispersing and nesting, which should help guide and improve conservation and management efforts to protect this species.

Our study is the first that focuses on sex-biased natal dispersal within Black Skimmers, but it does have several limitations. All three natal colonies were from one region in southwest Florida and future research should include colonies throughout more of their range. We did not find evidence that the more human disturbed colonies (St. Pete Beach and Indian Shores) had a higher proportion of banded birds dispersing than the less disturbed Clearwater Point colony, but it would be interesting to conduct a more in-depth analysis of the roles that disturbance, predation, and colony reproductive success have on the proportion of males and females that disperse.

Acknowledgments:

We thank the Eckerd College Ford Scholar Program for funding this research, as well as the Audubon Florida Bird Steward Program and the Florida Shorebird Alliance for their commitment to collecting Black Skimmer data. In addition, this project would not have been possible without the data gathered by citizen science from these organizations. Black Skimmers were captured and marked under M. Korosy's (23627), and E. Forsy's (24258) federal bird banding permits.

Data Availability:

All the relevant data appear in Appendix 1.

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Appendix 1. Descriptive data including sex, natal colony, dispersal colony where the Black Skimmers (*Rynchops niger*) were observed breeding for the first time, age at first breeding, and the distance between dispersal and natal colonies (i.e., dispersal distance).

Band	Year Banded	Sex	Natal Colony	Location of 1 st Breeding	Age of 1 st Breeding (yrs)	Presence of Natal Dispersal?	Dispersal Distance (km)
A01	2015	Male	Indian Shores	Indian Shores	2	No	0.00
A02	2015	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
A04	2015	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
A06	2015	Male	St. Pete Beach	Lido Key	3	Yes	50.04
A07	2015	Male	St. Pete Beach	St. Pete Beach	3	No	0.00
A09	2015	Female	St. Pete Beach	Clearwater Point	2	Yes	27.22
A13	2015	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
A16	2015	Female	St. Pete Beach	Indian Shores	2	Yes	16.35
A20	2015	Female	St. Pete Beach	Indian Shores	3	Yes	16.35
A22	2015	Male	St. Pete Beach	Lido Key	3	Yes	50.04
A25	2015	Male	St. Pete Beach	Lido Key	3	Yes	50.04
A27	2015	Female	St. Pete Beach	Lido Key	2	Yes	50.04
A29	2015	Male	St. Pete Beach	Carlos Point	3	Yes	168.68
A33	2015	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
A35	2015	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
A39	2015	Male	Indian Shores	3D	3	Yes	40.55
A43	2015	Female	Indian Shores	St. Pete Beach	2	Yes	16.35
A44	2015	Male	Indian Shores	Indian Shores	2	No	0.00
A46	2015	Female	Indian Shores	St. Pete Beach	2	Yes	16.35
A55	2016	Female	Indian Shores	St. Pete Beach	3	Yes	16.35
A56	2016	Female	Indian Shores	Lido Key	3	Yes	66.64
A75	2016	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
A76	2016	Male	St. Pete Beach	Lido Key	3	Yes	50.04
A77	2016	Male	St. Pete Beach	Lido Key	2	Yes	50.04
A79	2016	Female	St. Pete Beach	Lido Key	3	Yes	50.04
A83	2016	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
A90	2016	Male	St. Pete Beach	Clearwater Point	2	Yes	27.22
A91	2016	Male	St. Pete Beach	3D	3	Yes	32.71
A92	2016	Female	St. Pete Beach	Lido Key	3	Yes	50.04
A93	2016	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
A97	2016	Female	St. Pete Beach	Egmont Key	3	Yes	15.25
B05	2017	Male	Indian Shores	Caxambas Pass	3	Yes	242.64
B08	2017	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
B10	2017	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
B12	2017	Male	Indian Shores	Indian Shores	2	No	0.00

B18	2017	Male	Clearwater Point	Three Rooker	3	Yes	17.15
B19	2017	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
B20	2017	Male	Clearwater Point	Lido Key	2	Yes	76.50
B22	2017	Male	Clearwater Point	Clearwater Point	3	No	0.00
B23	2017	Female	Clearwater Point	Clearwater Point	3	No	0.00
B24	2017	Male	Clearwater Point	Clearwater Point	3	No	0.00
B28	2017	Male	Clearwater Point	Indian Shores	2	Yes	12.91
B30	2017	Male	Clearwater Point	Indian Shores	2	Yes	12.91
B31	2017	Female	St. Pete Beach	Stump Pass	4	Yes	101.29
B32	2017	Male	Clearwater Point	Indian Shores	2	Yes	12.91
B33	2017	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
B34	2017	Male	St. Pete Beach	Lido Key	2	Yes	50.04
B35	2017	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
B36	2017	Female	St. Pete Beach	Indian Shores	2	Yes	16.35
B38	2017	Female	St. Pete Beach	Patrick Airforce Base (roof)	3	Yes	217.97
B39	2017	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
B42	2017	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
B43	2017	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
B48	2017	Male	St. Pete Beach	Indian Shores	3	Yes	16.35
B50	2017	Male	St. Pete Beach	Egmont Key	4	Yes	15.25
B62	2018	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
B63	2018	Female	St. Pete Beach	St. Pete Beach	2	No	0.00
B66	2018	Male	St. Pete Beach	St. Pete Beach	3	No	0.00
B68	2018	Male	St. Pete Beach	Marco Island	2	Yes	221.26
B70	2018	Male	St. Pete Beach	St. Pete Beach	2	No	0.00
B72	2018	Male	St. Pete Beach	Clearwater Point	3	Yes	27.22
B74	2018	Male	Indian Shores	Indian Shores	2	No	0.00
B76	2018	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
B78	2018	Male	Indian Shores	Indian Shores	3	No	0.00
B79	2018	Male	Indian Shores	Indian Shores	3	No	0.00
B80	2018	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
B86	2018	Male	Indian Shores	Clearwater Point	2	Yes	12.91
0B	2019	Male	Indian Shores	Carlos Point	3	Yes	220.00
0C	2019	Male	Clearwater Point	Indian Shores	3	Yes	15.90
0D	2019	Female	Clearwater Point	Indian Shores	3	Yes	15.90
1D	2019	Female	Indian Shores	Three Rooker	3	Yes	32.20
3A	2019	Male	Indian Shores	Indian Shores	2	No	0.00
3B	2019	Male	St. Pete Beach	Lido Key	3	Yes	50.04
4A	2019	Male	St. Pete Beach	Lido Key	3	Yes	50.04
4B	2019	Male	St. Pete Beach	St. Pete Beach	3	No	0.00

4E	2019	Female	Clearwater Point	Longboat Key	3	Yes	61.20
5B	2019	Female	St. Pete Beach	Lido Key	2	Yes	50.04
6A	2019	Female	St. Pete Beach	Lido Key	2	Yes	50.04
6B	2019	Female	St. Pete Beach	Indian Shores	2	Yes	16.35
7B	2019	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
8A	2019	Male	Indian Shores	Lido Key	2	Yes	66.64
8B	2019	Female	Indian Shores	St. Pete Beach	2	Yes	16.35
B91	2019	Male	Indian Shores	St. Pete Beach	2	Yes	16.35
B92	2019	Male	St. Pete Beach	Clearwater Point	2	Yes	27.22
B93	2019	Male	Clearwater Point	Clearwater Point	2	No	0.00
B96	2019	Male	St. Pete Beach	Indian Shores	3	Yes	16.10